Inverse-solution method for a class of non-classical cochlear models

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Measurements of distortion-product (DP) waves inside the cochlea have led to a conception of wave propagation that is at variance with the “classical” attitude. Of the several alternatives that have been proposed to remedy this situation, the feed-forward model could be a promising one. This paper describes a method to apply the inverse solution with the aim to attain a feed-forward model that accurately reproduces a measured response. It is demonstrated that the computation method is highly successful. Subsequently, it is shown that in a feed-forward model a DP wave generated by a two-tone stimulus is almost exclusively a forward-traveling wave which property agrees with the nature of the experimental findings. However, the amplitude of the computed DP wave is only substantial in the region where the stimulation patterns of the two primary tones overlap. In addition, the model developed cannot explain coherent reflection for single tones. It has been suggested that a forward transversal DP wave induced by a (retrograde) compression wave could be involved in DP wave generation. This topic is critically evaluated.

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I. INTRODUCTION

Models of cochlear mechanics usually consist of a dual fluid-filled channel of which the parts are separated by a flexible partition. The solution of the model equation then represents the equilibrium between the hydrodynamics of the fluid and the dynamics of the partition—which is dominated by the basilar membrane (BM) and the cells of the organ of Corti. In a “classical” model, the mechanical properties of the cochlear partition depend only on the *local* longitudinal coordinate. Classical models have abundantly been used for a great variety of purposes. “Non-classical” models contain mechanical properties that depend on variables at more than one location. Such models have been used to explain properties that could not be explained by a classical model. In the field of non-classical models, feed-forward models have been considered in more detail (a few examples: [Steele et al., 1993](#); [Geisler and Sang, 1995](#); [Wen and Boahen, 2003](#)). In a feed-forward model, the pressure at location x depends on the velocity at the same location (the “passive” or classical component of the dynamics) as well as on the velocity at location $x - \Delta x$ (the non-classical component) where Δx is a positive constant—generally taken to be equal to several times the diameter of an outer hair cell (OHC). This type of model has unique properties in its modes of wave propaga-

tion ([de Boer, 2007](#)) which makes it suitable to explain wave-propagation properties of observed distortion products (DPs) (for specific references, see further on). To clarify why this would be important, a few descriptive steps have to be taken.

Step 1: A classical model. The response of the viable, living cochlea is quite different from that of the *postmortem* cochlea. This implies that the dynamics of the cochlear partition is quite different in these two cases. In the *postmortem* cochlea, the BM has passive properties; its dynamics can be described by an impedance which has stiffness and mass, and a positive resistance. In the living cochlea, an additional mechanism causes the response to show a pronounced peak, and when we assume linearity, this effect can be described by an additional component, the “active” component, of the BM impedance. It is generally agreed that the effects of this additional impedance are caused by OHCs; the precise manner in which these cells perform their task is greatly unknown at present. One factor involved may be the mechanical action of the Internal Spiral Sulcus, as described in the literature, see [de Boer \(1993\)](#) and [Steele and Lim \(1999\)](#). A possible mechanism taking care of the necessary frequency selectivity may reside in resonance of the tectorial membrane, see, e.g., [Neely and Kim \(1986\)](#) for a model based on ideas by [Allen \(1980\)](#) and [Zwislocki and Kletskey \(1979\)](#). [de Boer \(1996\)](#), [Patuzzi \(1996\)](#), and [Robles and Ruggero \(2001\)](#) have written reviews. It is repeated that in this context the cochlear model, including the action of the OHCs, is assumed linear.

Step 2. When the cochlea is stimulated by two primary

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tones, with frequencies f_1 and f_1 , the OHCs, being intrinsically nonlinear physiological transducers, will generate harmonic components with the same frequencies and their multiples, but also intermodulation components, which we will term DPs. These DPs are mainly generated in the *overlap region* which is the region where the excitation patterns of the two primary tones overlap. One of the most important of those DPs has the frequency $2f_1 - f_2$. From the overlap region, two waves with the DP frequency are assumed to originate. One travels toward the helicotrema, and the other one toward the stapes. Physically, these two waves should have the same or closely related propagation properties. However, in experiments, they manifest themselves quite differently. The apical DP wave is easily observable but the reverse DP wave is not. In fact, where one would expect that reverse wave to exist, between the overlap region and the stapes, it is impossible or hard to find. In that region a forward wave dominates (Ren, 2004; He *et al.*, 2007, 2008; de Boer *et al.*, 2008; Dong and Olson, 2008). This curious phenomenon forms a challenge to theorists.

Step 3. One of the theories advanced to explain this property involves feed-forward. As has been observed (Steele *et al.*, 1993) and proven rigorously (de Boer, 2007), the mechanism of feed-forward, when adjusted to show wave amplification for forward-traveling waves, demonstrates wave attenuation for reverse waves. That is, the propagation of a reverse wave differs from that of a forward wave. Finding out the main characteristics of cochlear models with feed-forward (and feed-backward) with respect to measured data forms the main topic of the present paper.

Step 4. Another explanation of the anomalous direction of wave propagation of DP waves has been brought forward; it involves compression waves (Ren, 2004). Briefly, the proposed mechanism is as follows. In the region of overlap, the OHCs form a large number of tiny sound sources oscillating with the DP frequency. Together all these sources give rise to a compression wave in the fluid. Ideally, that wave has an infinite velocity of propagation, and it invades all tissues and spaces of the inner ear instantly. The mechanism by which a compression wave turns into a transversal wave is the same as that by which we hear bone-conducted sound. The compression wave reaches the region of the oval and round windows. Because the mechanical impedances of the two membranes are quite different, the two membranes will start to oscillate with different velocities. As a result, a “normal” propagating wave starts at the windows, having the DP frequency as its frequency. A short discussion of compression waves is included in this paper.

In earlier work of the present authors, the *inverse-solution method* (de Boer, 1995a, 1995b; de Boer and Nuttall, 1999) has been used for several purposes (e.g., to explain intensity effects: de Boer and Nuttall, 2000; to assess tones versus noise stimuli: de Boer and Nuttall, 2002; to analyze spontaneous oscillations of the BM: de Boer and Nuttall, 2006b; to analyze general wave-propagation properties: de Boer *et al.* 2007). In the inverse solution, the mechanical impedance of the BM is derived from a given BM response curve. That work was always centered at a classical cochlear model.

In the present study, it is shown how the inverse method can be extended to a feed-forward model. This application will result in a non-classical model, a feed-forward model, which is shown to provide an accurate reproduction of the response actually measured in a physiological experiment. An application in a different sense is illustrated for the case of a DP wave generated by nonlinear distortion of OHCs. This extension forms the main theme of the present work. Discussion of feed-backward and combination of feed-forward with feed-backward is beyond the scope of this paper.

II. DERIVATION: THE INVERSE SOLUTION

We will first consider the case of the classical, linear model, with two fluid-filled channels. In such a model, the local velocity of the BM only depends on the local pressure difference across it, and not on influences from elsewhere, from other locations. In that case the mechanics of the organ of Corti is lumped into the concept of a mechanical impedance (a point-impedance), called the BM impedance Z_{BM} . This impedance relates (in a way to be detailed further on) the pressure across the BM at a point x along the length of the BM to the velocity of the BM at the *same* location x . That impedance, obviously a function of location x , is converted into a diagonal matrix $\mathbf{Z}_{BM}$. In this step we have tacitly replaced the continuous variable x by a finite sequence of N samples. The model equation then reads (de Boer *et al.*, 2007):

$$(i\omega\rho\mathbf{G} + \frac{1}{2}\mathbf{Z}_{BM})\mathbf{v} = -i\omega\rho\mathbf{S}v_{st}. \quad (1)$$

The matrix $\mathbf{G}$ of size $N \times N$ (which constitutes the Green’s function) represents the hydrodynamics of the fluid inside the model. The vector $\mathbf{S}$ (a column vector) is the stapes propagator (see Mammano and Nobili, 1993) and v_{st} is the stapes velocity. The “stylized” model of the cochlea has the form of a rectangular block in which the BM occupies a fraction (in our case 0.2) of the width, as in earlier work (de Boer, 1995a, 1995b). From Eq. (1) the BM velocity $\mathbf{v}$ (again a column vector) can be solved for a given form of $\mathbf{Z}_{BM}$ —this constitutes the *forward* solution.

The normal procedure of the *inverse* solution consists of two parts. First, from the given BM velocity $\mathbf{v}$ the pressure $\mathbf{p}$ that is solely due to hydrodynamics is determined. Normally, this is formed from the combination of the first term and the right-hand member of Eq. (1):

$$\mathbf{p} = i\omega\rho\mathbf{G}\mathbf{v} + i\omega\rho\mathbf{S}v_{st}. \quad (2)$$

It is important to notice that the pressure $\mathbf{p}$ is solely determined by the hydrodynamics of the fluid because the matrix $\mathbf{G}$ and the vector $\mathbf{S}$ solely depend on the geometry of the bony shell of the cochlea. In the second step the effective BM impedance Z_{eff} is determined from the so-computed pressure $\mathbf{p}$ and the (given) BM velocity $\mathbf{v}$ (all variables are tacitly considered to be functions of location x):¹

$$Z_{\text{eff}} = -2p/v. \quad (3)$$

In fact, Z_{eff} is a function of location x , but for reasons of clarity and simplicity we will omit the dependence on x from our equations wherever that is feasible.

To verify the accuracy of the procedure, the *resynthesized response* of the model is computed by substituting the derived impedance Z_{eff} , converted into a diagonal matrix $\mathbf{Z}_{\text{eff}}$, into the model Eq. (1) and solving that equation for $\mathbf{v}$. Because an inverse solution is known to be like an “ill-posed problem,” this step is not superfluous (for more details on resynthesis see [de Boer and Nuttall, 1999](#)).

It should now be recognized that the so-derived BM impedance Z_{eff} is composed of a passive part that represents the impedance of the BM in the *postmortem* cochlea and an active part that induces the response of the viable cochlea to deviate so drastically from the *postmortem* response. This distinction is of prime importance.

In a *feed-forward* model, the OHC contribution from the BM velocity at location x results in an added pressure at location $(x+\Delta x)$, where Δx is positive. Assume, for a moment, that this is the only effect of the dynamics of the BM; this means that we temporarily omit the mechanical dynamics of the (passive) BM. Introduce X_{ffw} (tacitly assumed to be a function of x) to express the coefficient with which the local velocity has to be multiplied to find the associated (shifted) pressure, in an analogous way as Eq. (3). The function X_{ffw} is recognized to be a transfer impedance. In essence, it is a continuous function of x but as before we will consider it as a finite sequence of N samples. In matrix language X_{ffw} is to be converted into an *off-diagonal* matrix $\mathbf{X}_{\text{ffw}}$; the diagonal is distant from the main diagonal by a number of steps that corresponds to Δx . When $\mathbf{X}_{\text{ffw}}$ contains elements below the main diagonal, we have feed-forward, when it contains elements above the main diagonal, we have feed-backward. If Eq. (3) is rewritten as $p = -\frac{1}{2}Z_{\text{eff}}v$, it is easy to see that the product $\frac{1}{2}\mathbf{X}_{\text{ffw}}\mathbf{v}$ relates the (shifted) OHC-generated pressure to the velocity $\mathbf{v}$. The model equation then becomes

$$(i\omega\rho\mathbf{G} + \frac{1}{2}\mathbf{X}_{\text{ffw}})\mathbf{v} = -i\omega\rho\mathbf{S}\mathbf{v}_{\text{st}}, \quad (4)$$

in complete analogy to Eq. (1).² In the forward solution, it is this equation that has to be solved for $\mathbf{v}$.

In the feed-forward case, the first step of the inverse solution is identical to that in a classical model: the pressure $\mathbf{p}$ is computed from the hydrodynamic equation (2). Note again that this step only involves hydrodynamical concepts, the matrix $\mathbf{G}$ and the vector $\mathbf{S}$. The second step of the inverse solution is different because the vectors $\mathbf{v}$ and $\mathbf{p}$ do not refer to the same points on the x -axis. Dividing the *shifted* pressure p by the unmodified velocity v produces the function X_{ffw} , in an analogous fashion as Z_{eff} in Eq. (3). This is the feed-forward impedance function which, transformed into an off-diagonal matrix $\mathbf{X}_{\text{ffw}}$ and used in the model Eq. (4), should produce an accurate replica of the original given BM velocity $\mathbf{v}$. This elaboration forms the core of the feed-forward inverse solution and the associated resynthesis.

Actually, the situation is somewhat more complicated. We must take into account that the BM in the model has an

inherent passive mechanical component that is not influenced by actions of OHCs. For reasons of simplicity, we will assume that this component is not involved in any form of feed-forward and that it can be represented by a classical impedance, called the passive BM impedance. This impedance has to be included in our inverse procedure but it has to remain outside the feed-forward process. Call that impedance function Z^{pass} and its associated diagonal matrix $\mathbf{Z}^{\text{pass}}$. Redefine the pressure $\mathbf{p}$ as follows:

$$\mathbf{p} = (i\omega\rho\mathbf{G} + \frac{1}{2}\mathbf{Z}^{\text{pass}})\mathbf{v} + i\omega\rho\mathbf{S}\mathbf{v}_{\text{st}}. \quad (5)$$

It is this pressure that has to be produced by the feed-forward impedance X_{ffw} . Equation (5) is the analog of Eq. (2) for the case where the classical passive BM impedance is explicitly included. The pressure $\mathbf{p}$ according to Eq. (5) is, in shifted form, divided by $\mathbf{v}$ to yield the transfer impedance X_{ffw} . Convert this impedance to an off-diagonal matrix $\mathbf{X}_{\text{ffw}}$ and substitute it into the “complete” model equation:

$$(i\omega\rho\mathbf{G} + \frac{1}{2}(\mathbf{Z}^{\text{pass}} + \mathbf{X}_{\text{ffw}}))\mathbf{v} = -i\omega\rho\mathbf{S}\mathbf{v}_{\text{st}}. \quad (6)$$

This equation can be solved for $\mathbf{v}$. Note that $\mathbf{Z}^{\text{pass}}$ is a diagonal and $\mathbf{X}_{\text{ffw}}$ an off-diagonal matrix. The so-obtained resynthesized response should be a good approximation of the given BM velocity with which the inverse procedure was started. It has been our experience that in the feed-forward case the inverse method is more prone to errors than in the classical case. Therefore, the resynthesis step is really essential.

From the above derivation, it should be clear that $\mathbf{Z}^{\text{pass}}$ does not necessarily have to be the passive BM impedance, measured *postmortem*. It can be any impedance that behaves as a point-impedance, i.e., any impedance that relates pressure to velocity at the same location. In fact, it can be a combination of the actual passive BM impedance and a fraction of the (classical) active component of the effective BM impedance. In that way any “degree” of feed-forward can be built in (from 0 to 100%), and in that respect, the inverse-solution method outlined above is quite universal. In the present paper, we will leave that extension unexplored, to preserve space, and we will consider only the passive component of the BM impedance to be separated out in the classical sense as in Eqs. (5) and (6).

III. EXAMPLE I: FEED-FORWARD—SINGLE TONES

Responses were measured at the BM of the guinea pig, with the beam of a laser interferometer directed at a location on the BM that has a best frequency (BF) in the range from 16 to 20 kHz. The measurement method has been described before ([de Boer and Nuttall, 2000](#)). The protocols of the experiments, which were performed on deeply anesthetized animals, were approved by the Oregon Health & Science Committee on the Use and Care of Animals and consistent with NIH guidelines for humane treatment of animals. For the single-tone stimulus case, we utilized responses measured at low levels, of the order of 20–40 dB sound pressure level (SPL), and responses of the same cochlea measured *postmortem*. Responses are measured as functions of frequency and have been converted into “cochlear patterns,”

FIG. 1. Result of resynthesis in the single-tone case. Length of the model: 12 mm, divided into 1024 segments. Parameters of model are derived from an experiment. Frequency: 17 kHz. The passive component of the BM impedance has been determined from the *postmortem* response of the same animal, and the remainder of BM dynamics is interpreted in terms of feed-forward (see Eqs. (5) and (6)). Full-drawn and finely dotted curves: original response, amplitude (scale on the left), and phase (scale on the right). Coarsely dotted curves: resynthesized response, amplitude, and phase. For clarity, the amplitude of the resynthesized response has been plotted 2 dB lower than the original amplitude. This figure illustrates the fidelity of the sequence inverse-solution-resynthesis in the feed-forward model.

i.e., response functions as functions of the location variable x , valid for one frequency (usually chosen to be equal to the BF corresponding to a low-level response). A standard frequency-location map has been used in the conversion, refinements of the mapping procedure are described in de Boer and Nuttall (1999). For the two-tone computations (Sec. IV), we assume that the model is stimulated by two fairly strong tones of which we know the excitation patterns. In that case, we estimate the distribution of DP sources for third-order

distortion occurring in the OHCs—in the same way as we have done before (de Boer *et al.*, 2007).

By way of Fig. 1, we illustrate the fidelity of the inverse solution in the case where one component of BM dynamics is contained in the *postmortem* impedance Z^{pass} and the other part involved in the feed-forward process. That is, we have used Eq. (5) as the basis of the inverse solution and Eq. (6) for resynthesis. The model has a length of 12 mm (of which only a part is shown), divided into 1024 sections. The feed-forward distance Δx has been given the value $23 \mu\text{m}$. For clarity the resynthesized amplitude is drawn 2 dB below the original amplitude curve; the two phase curves coincide over most of their ranges, and are seen to depart from one another where the amplitude has dropped more than 50 dB from its peak.

The example of Fig. 1 has been selected because of its almost ideal resynthesis. More realistic cases are presented by Fig. 2 which shows results of four experiments, in four different animals. Again it is evident that the resynthesized response curves are good imitations of the original responses. However, there is more variability in and between the data sets, but that is mainly outside the main response region. We conclude that the inverse solution is sufficiently accurate for our further needs. We will now use this method to predict the behavior of DP waves in a feed-forward setting.

IV. EXAMPLE II: FEED-FORWARD—TWO STIMULUS TONES AND DPS

Let us consider the case where the model is stimulated by two tones, with frequencies f_1 and f_2 . These tones are presented with an intermediate intensity; we will call the appropriate response functions $v^{(1)}$ and $v^{(2)}$. Again we have

FIG. 2. Results of inverse solution followed by resynthesis in four different experiments. Parameters of the model are derived from these experiments. Tone frequency: 17 kHz. The amplitude of the resynthesized wave is drawn 2 dB lower than the original amplitude.

omitted the dependence on location x . For each of the two tones, the corresponding transfer impedance X_{ffw} can be determined; call these two functions $X_{\text{ffw}}^{(1)}$ and $X_{\text{ffw}}^{(2)}$. It is repeated that both functions only represent the OHC-controlled components of the BM dynamics; the passive component Z^{pass} has been separated out. The transfer impedances $X_{\text{ffw}}^{(1)}$ and $X_{\text{ffw}}^{(2)}$ as well as the passive components Z^{pass} refer to the two different frequencies, f_1 and f_2 , respectively. A product $p_{\text{act}}^{(1)}$ like

$$p_{\text{act}}^{(1)} = -\frac{1}{2}v^{(1)}X_{\text{ffw}}^{(1)} \quad (7)$$

will now represent the active pressure developed by the hair cells due to tone 1 for the frequency f_1 . Similarly, $p_{\text{act}}^{(2)}$ defined by

$$p_{\text{act}}^{(2)} = -\frac{1}{2}v^{(2)}X_{\text{ffw}}^{(2)} \quad (8)$$

will represent the OHC pressure corresponding to tone 2 for the frequency f_2 . In both products, the displacement Δx has to be taken into account, of course.³ In the limit of small nonlinear distortion, the DP with frequency $2f_1 - f_2$ will appear in the output of the OHCs with an amplitude $A_{\text{DP}}(x)$ given by (for more details, see [de Boer et al., 2007](#))

$$A_{\text{DP}}(x) = A(p_{\text{act}}^{(1)}(x))^2 \cdot (p_{\text{act}}^{(2)}(x))^*, \quad (9)$$

where we have deliberately reintroduced the independent variable x . It is recalled that $p_{\text{act}}^{(1)}(x)$ and $p_{\text{act}}^{(2)}(x)$ refer to the same x -axis but intrinsically contain information about two different frequencies, f_1 and f_2 . In contrast, the resulting coefficient $A_{\text{DP}}(x)$ describes the complex amplitude for a wave with the DP frequency f_{DP} equal to $2f_1 - f_2$. The square in Eq. (9) arises because the expression for f_{DP} contains the term $2f_1$, the superscript asterisk (*) denotes the complex conjugate and is needed because the DP frequency contains the term $-f_2$. The multiplier A will be specified further on. It is stressed that Eq. (9) implies that the drive behind the DP wave, as it is expressed by the pressure $A_{\text{DP}}(x)$, is solely due to physiological effects produced by viable OHCs (as in our earlier work on DP waves, [de Boer et al., 2007](#)). That we are again using the case of small nonlinear distortion is based on the fact that experiments on DP waves have yielded consistent results for stimulus signals as weak as 40 and 50 dB SPL ([He et al., 2007](#)).

The pressure distribution $A_{\text{DP}}(x)$ acts as a source distribution for the resulting DP wave, with the DP frequency equal to $2f_1 - f_2$. That DP wave can now be computed from a small variation in the model equation, Eq. (6), where the stapes excitation term $-i\omega p S v_{\text{st}}$ is replaced by the column vector $\mathbf{A}_{\text{DP}}$ which represents $A_{\text{DP}}(x)$. The resulting equation reads

$$(i\omega p \mathbf{G} + \frac{1}{2}(\mathbf{Z}^{\text{pass}} + \mathbf{X}_{\text{ffw}}))\mathbf{v} = +\mathbf{A}_{\text{DP}}. \quad (10)$$

All terms are to be evaluated at the DP frequency f_{DP} . The transfer impedance X_{ffw} is determined from a measured tone response of the animal, at the lowest feasible level (usually 20 dB SPL). The passive impedance Z^{pass} is determined from the *postmortem* response, at the highest level (100 dB). Both of these parameters are evaluated for the DP frequency and

are functions of location x . For the computation of $A_{\text{DP}}(x)$ (see Eq. (9)), responses and impedances are used for higher levels, adapted to the appropriate frequencies, f_1 and f_2 . For the method to reduce reflection of the DP wave at the stapes end, we refer to [de Boer et al. \(2007\)](#).

Figure 3 shows four representative theoretical results computed from results of four experiments. Two tones of 40 dB SPL with frequencies f_1 and f_2 , with the frequency ratio equal to 1.08, were used as stimuli. The amplitudes of the excitation patterns produced by these tones are shown by dashed curves (labeled: f_1 and f_2) and suggested by shading. The levels at which these patterns are plotted are arbitrary; they are selected for visual clarity. The resulting DP waves are computed as described above. In each panel, the solid thick curve shows the amplitude of the computed DP wave and the coarsely dashed curve shows the phase; the scale for the amplitude appears on the left, that for the phase on the right. The amplitude factor A in Eq. (9) has been selected so that in the region of maximum response to the DP frequency, the amplitude is around 50 dB.

Figure 3 shows results for the same experiments as used for the publication at the Keele Symposium ([de Boer and Nuttall, 2008](#)), produced with a small variation in the original program. Figure 4 shows results, plotted in the same layout, for a further set of four animals. In this case the results show somewhat more variability. It should be remembered that the “best” results of computations are usually obtained from experiments that yield “smooth” impedance curves; in the present cases more realistic results are shown. It should be clear that a considerable part of the DP wave propagates in the forward direction. In addition, this property is evident also outside the region where the amplitude of the DP wave is substantial, and that is the main result of the present study. There are irregularities in the phase curves but in no case is a clear reverse wave present near or not far from the stapes. As an afterthought, it is quite surprising that a feed-forward effect, active over a distance of just a few hair-cell diameters, and only present in the active region of the cochlea, can have such a profound effect, even on small-amplitude waves at a considerable distance.

V. ABOUT THE DP COMPRESSION WAVE

We were inspired to study feed-forward (and its variations) by the results from measurements on the DP wave, both inside the cochlea (see the references mentioned in Sec. I) and outside it, in the form of otoacoustic emissions ([Ruggero, 2004](#); see also [Siegel et al., 2005](#)). As stated in Sec. I, it has been attempted by some authors to explain these findings by a mechanism that invokes a compression wave. That explanation has been criticized on several grounds, notably on its inability to explain frequency-and-location-selective “activity” ([de Boer and Nuttall, 2006a](#)) and its failure to explain the Allen–Fahey effect ([Shera et al., 2007](#); [Shera and Guinan, 2007](#)). In other words, it cannot be the compression wave that induces propagation of DP waves in the cochlea. (To quote Shakespeare’s Hamlet: “There are more things in heaven and earth, Horatio, than are dreamt of in your philosophy.”) In all that work, the background of the elabora-

FIG. 3. DP waves generated in a stylized three-dimensional model with feed-forward. Two tones of 40 dB SPL with frequencies f_1 (14.57 kHz) and f_2 (15.74 kHz) are used as stimuli. The amplitudes of the excitation patterns produced by these tones are shown by dashed curves (labeled f_1 and f_2) and suggested by shading. Generation of the DP wave with frequency $2f_1 - f_2$ (13.41 kHz) computed as described in de Boer *et al.* (2007), and further described in the text. Reflection of the DP wave at the stapes has been suppressed. Solid thick curve: amplitude of the resulting DP wave. Ordinate scale on the left. Coarsely dashed curve: the associated DP phase response, scale on the right. The thick and the thin dotted curves show amplitude and phase, respectively, of the response to a single low-level tone with the DP frequency started at the stapes. These curves serve as landmarks.

tions has been a classical model of the cochlea. We presently want to discuss the effect of a compression wave in a feed-forward model, but we should keep in mind the reservations expressed in the cited papers.

The main point is this: In the cases we have shown in Figs. 3 and 4 the computed DP wave generated by the feed-forward mechanism is extremely small in the region between the stapes and the primary-tone response patterns. It is so small that whatever is the amplitude of the *compression-induced wave* (in the sequel to be called CI-W), the latter will be dominant in most of that region. This type of DP wave would then be the only source of otoacoustic emissions and also control what we observe inside the cochlea. For this reason (and for this reason only, see the above-mentioned counter-arguments and restrictions), we will present an estimate of the CI-W in our model.

The compression-induced DP wave has been analyzed in Shera *et al.* (2007), and we accept the main idea. We will assume that $A_{DP}(x)$ given by our Eq. (9) is also the source distribution of the compression wave. In this way, we will be able to compare the CI-W directly with the DP wave considered in Sec. IV.

Two compression waves arise from the overlap region, one toward the helicotrema and one toward the stapes. In

theoretical exercises, the fluid is usually considered incompressible. In a more practical situation, the fluid is compressible and the speed of sound in it finite. In fact, for frequencies around 17 kHz, the length of the guinea-pig cochlea is of the order of a quarter wavelength. This means that for a high frequency the basally generated compression wave encounters an obstacle. The essentially very large impedance of the top of the cochlea (it is all bone) is transformed into a small impedance in the region where the compression wave is generated. Therefore, we must expect that the apical part of the compression wave “shunts” the basal part so that the latter arises from a smaller pressure than $A_{DP}(x)$. If we take $A_{DP}(x)$ as the source and compute a compression-induced DP wave from it, we are decidedly *over-estimating* the basal compression wave. Here we end our short excursion into the domain of finite compressibility of the fluid. In the sequel, we consider only an ideal fluid.

Integration over space yields the pressure p_{evo} that drives the compression wave:

$$p_{evo} = \int_0^L A_{DP}(x) dx, \quad (11)$$

where L denotes the length of the model.⁴ As said, from here

FIG. 4. Same as Fig. 3, with a different selection of animals. In these cases, the results display more variability.

on we again assume the compression wave to have an infinite velocity of propagation; hence p_{evo} is the same everywhere. At the location of the stapes, the compression wave is equal to p_{evo} . If we divide the pressure p_{evo} by the effective input impedance of the cochlea (the impedance loading the oval window), we obtain the equivalent stapes velocity (at least, if we ignore the impedance of the round window, see [Shera et al., 2007](#)). The input impedance of the model can easily be found from our computations. To this impedance, another impedance must be added: the radiation impedance representing the sound that is going to the outer world, via the middle ear. For simplicity, we assume this impedance to be equal to the aforementioned input impedance—implying an ideal impedance match between cochlea and middle ear. This reduces the amplitude of the CI-W by 6 dB. It should finally be recalled that all variables involved must be computed for the DP frequency.

Figure 5 shows four representative results. The figure shows the amplitudes of the computed CI-Ws. These amplitudes are normalized in exactly the same way as the DP waves. As a result, the panels display the relation between the CI-W and the “regular” feed-forward DP wave. It is clear that there is considerable variation between the panels; we have selected experiments from the sets shown in earlier figures to demonstrate the extremes of the CI-W. It is also clear that in the region where the DP frequency shows its own maximum, the DP wave and the CI-W are of comparable magnitude. The figure confirms what has been said above:

outside the main region of the DP wave it is the CI-W that dominates. With respect to direction of propagation, there is no difference. However, because the CI-W does not have the required properties (see above), we should see these results only as indicative, not as final outcomes. At any rate, the figures show the relation between the amplitudes of the computed CI-W and the regular feed-forward DP wave correctly, because they have been derived from the same DP source function $A_{\text{DP}}(x)$ and plotted with the same normalization factor. We should recall that the compression wave can directly be identified in experiments on intra-cochlear pressure ([Dong and Olson, 2008](#) and earlier work). It was found that the Distribution Product Oto-Acoustical-Emission (DPOAE) related to the compression wave is “Much lower than the actual DPOAE we have measured in the ear canal” (citation from *loc. cit.*).

VI. EXPLANATIONS, CONCLUSIONS, LIMITATIONS

The main property that emerges from Figs. 3 and 4 is that the computed DP wave is almost exclusively a forward wave, over most of its range. The theory described in [de Boer \(2007\)](#) yields that forward and reverse waves have quite different amplification properties, but that theory is only valid in a structure exclusively governed by feed-forward. Apparently, it is also valid in the case where the passive component of the BM impedance is included.

FIG. 5. In addition to the DP wave, the CI-W is shown. Only the amplitude of that wave is shown (the phase follows that of a simple tone at the same frequency injected at the stapes). Experiments have been selected to show “normal” as well as “large” amplitudes of that wave. It has been assumed that the middle ear is loaded by the same impedance as the input impedance of the cochlea. The short-circuit effect of the apical part of the CI-W (see text) has been neglected.

Where the DP wave originates, in the region of overlap, both forward and reverse waves are initiated. Going to the left, toward the stapes, the reverse wave starts to be progressively attenuated in a feed-forward model. And still more to the left even the forward wave dwindles to a very small amplitude. One may ask the following questions: Why is not there a substantial forward wave in this region? Does not there exist some kind of effective stimulus here that would generate it? The answer is no. In this region, the DP drive pressure $A_{DP}(x)$ is too small to have an effect by itself. Secondary effects (due to hydrodynamics and the passive BM impedance) of that drive pressure have been found to remain restricted to the region where $A_{DP}(x)$ is maximal.

In effect, the theoretical prediction of a small forward-going DP wave in this region is contrary to experiment. In [de Boer et al. \(2008\)](#), it is shown that the forward-propagating character of the DP wave is present in almost all of the region between overlap region and stapes. A similar conclusion can be drawn from the other papers on this subject mentioned in Sec. I. Apparently, if feed-forward is a concept to be included in the explanation of the data, it has to be extended or modified. We recall what has been said about a possible combination of a classical and a feed-forward model at the end of Sec. II.

There is a further problem with the feed-forward concept. As demonstrated here, the principle of feed-forward

does not allow a sizable reverse DP wave to occur. The same would be true for any other (non-classical) type of reverse wave. As a consequence, the principle of coherent reflection cannot work in such a model. We further refer to the discussion of this topic in the Keele paper ([de Boer and Nuttall, 2008](#)), and await further theoretical developments. At this point, we can only add that a mechanism including a CI-W does not alleviate that problem. Only the extension of the feed-forward concept alluded to in the ending part of Sec. II can do that.

For the sake of completeness, we computed the CI-W, and found it to have all the properties we could have predicted. We did not pursue this topic any further because, from various sides, it can be argued that the CI-W cannot be the DP wave observed inside the cochlea and cannot be the source of DP otoacoustic emissions.

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¹The minus sign and the factor 2 are due to sign conventions. Upward movement of the BM is counted positive, p is the pressure in the upper channel, and $-p$ in the lower channel.

²Actually, in the resynthesis procedure, the stapes velocity should be replaced by the virtual stapes velocity (de Boer and Nuttall, 1999).

³It should be noted that the expression $\frac{1}{2}v^{(1)}X_{\text{ffw}}^{(1)}$ with shifted x -scales in the two factors is identical to the corresponding classical expression $\frac{1}{2}v^{(1)}Z_{\text{BMfact}}^{(1)}$ with equal x -scales, where $Z_{\text{BMfact}}^{(1)}$ is the "active" component of the classical BM impedance for tone 1. This can be seen by comparing Eq. (6) with its classical counterpart, Eq. (1). The same is valid for tone 2.

⁴At first sight, it may be confusing to observe that $A_{\text{DP}}(x)$ and p_{evo} have different dimensions. In fact, $A_{\text{DP}}(x)$ has the meaning of being a pressure density, the pressure produced by OHCs per unit of length.

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